Revision of the Archosauromorph Reptile Trilophosaurus, With a Description of the First Skull of Trilophosaurus Jacobsi, From the Upper Triassic Chinle Group, West Texas, Usa

By: **Andrew B. Heckert**, Spencer G. Lucas, Larry F. Rinehart, Justin A. Spielmann, Adrian P. Hunt & Robert Kahle

Abstract

The first abundant, well-preserved fossils of the unusual archosauromorph reptile Trilophosaurus jacobsi Murry are from an Upper Triassic bonebed in the lower-most Trujillo Formation of the Chinle Group in Borden County, Texas. A nearly complete left side of the skull and incomplete but articulated mandible of a juvenile individual demonstrate that Trilophosaurus jacobsi Murry is referable to Trilophosaurus, so the putative procolophonid genus Chinleogomphius is a junior objective synonym of Trilophosaurus. Features of T. jacobsi that diagnose it from T. buettneri include asymmetrical, tricuspate teeth in which the central cusp is taller than the marginal cusp, polygonal in cross-section and displaced slightly lingually; the lingual cusp is low, transversely broadened and anteroposteriorly compressed; teeth with prominent cingula along the mesial and distal margins; and paired sagittal (parasagittal) crests composed of portions of the postfrontals and the parietals, as well as a relatively broad skull roof between the supra-temporal fenestrae. We also re-illustrate and re-describe the holotypes of both Trilophosaurus buettneri Case and T. jacobsi Murry. T. jacobsi is primarily Adamanian in age, and the lowest occurrence of T. jacobsi is stratigraphically above that of T. buettneri. Therefore, T. buettneri is an Otischalkian–Adamanian index taxon, and T. jacobsi is an Adamanian–earliest Revueltian index taxon. Trilophosaurus teeth are readily identifiable to species and therefore iden-tifiable as isolated fossils.

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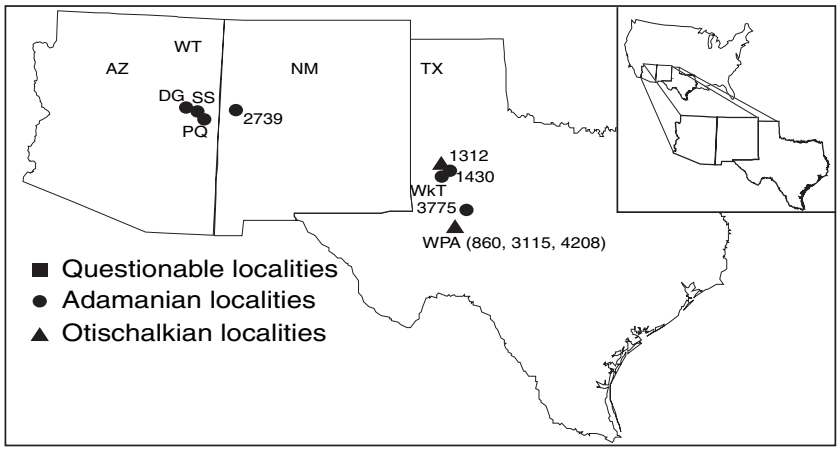
DURING Triassic time, continental tetrapod faunas changed in composition from temnospondyl- and primitive-synapsid-dominated Early Triassic faunas to archosaur-dominated Late Triassic faunas. An intriguing subplot that is often lost in discussion of this evolutionary transition is the changes that occurred in the nature of some specialized, herbivorous tetrapods. During the Early Triassic, procolophonids comprised a substantial proportion of the herbivorous fauna (as did dicynodonts and gomphodont cynodonts), whereas Late Triassic procolophonids are relatively rare, apparently having been supplanted by herbivorous archosauromorphs, including rhynchosaurs and trilophosaurs (e.g. Benton 1984, 1991; Reisz and Sues 2000). Rhynchosaurs are all but unknown in the Upper Triassic of North America (Hunt and Lucas 1991; Long and Murry 1995; Lucas *et al.* 2002), yet in places the trilophosaur *Trilophosaurus* is abundant. While rhynchosaurs have undergone significant revision in the past two decades (e.g. Benton 1983, 1984, 1990; Langer and Schultz 2000; Langer *et al.* 2000*a*, *b*), the less well-known trilophosaurs have had but one new taxon identified (Murry 1987), which was subsequently re-identified as a procolophonid (Sues and Olsen 1993). Even Late Triassic procolophonids in North America have received far more recent attention than trilophosaurs (Sues and Olsen 1993; Small 1997; Sues and Baird 1998; Sues *et al.* 2000).

Numerous workers have collected and described Upper Triassic fossils from various localities in West Texas, including Cope (1892), Case (1922, 1928*a*, *b*, 1932),



TEXT-FIG. 1. Index map showing the distribution of *Trilophosaurus* specimens in the Upper Triassic of the American West. State abbreviations: AZ, Arizona; NM, New Mexico; TX, Texas. Numbers refer to NMMNH locality numbers used in text. Locality abbreviations: DG, 'Dying Grounds', Petrified Forest National Park; SS, North Stinking Springs Mountain; WPA, Works Progress Administration quarries near Otis Chalk; WT, Ward's Terrace; WkT, Walker's Tank.

Gregory (1945), Murry (1982, 1986) and Chatterjee (1986) (Text-figure 1). Among the fossils collected were the original specimens of the unusual archosauromorph reptile *Trilophosaurus buettneri* Case, 1928*a*, subsequently the subject of a monograph by Gregory (1945) and described further by Parks (1969), DeMar and Bolt (1981) and Murry (1982). To date, almost all other verifiable *Trilophosaurus* records come from low in the Chinle Group in Texas (Gregory 1945; Parks 1969; Murry 1982, 1986; Heckert *et al.* 2001) or the Chinle Group in Arizona and New Mexico (Murry 1987; Murry and Long 1989; Long and Murry 1995). The only exceptions are isolated teeth collected by Kirby (1989, 1990, 1991, 1993) in the stratigraphically higher Owl Rock Formation of north-central Arizona (Text-fig. 1).

Here, we provide a detailed history of the study of *Trilophosaurus*, outline the stratigraphy of a new locality yielding fossils of *Trilophosaurus* and describe a nearly complete juvenile skull of *Trilophosaurus* from this locality. We also re-describe and re-illustrate the holotypes of *T. buettneri* and *T. jacobsi*, compare these with the referred fossils from the new locality, and comment on the biostratigraphical and biochronological significance of *Trilophosaurus*.

MATERIAL AND METHODS

For this paper, the principal fossils studied were an extensive collection of associated skulls, mandibles and postcrania at the New Mexico Museum of Natural History and Science (NMMNH) from NMMNH locality 3775 (Heckert *et al.* 2001). Additionally, we borrowed and examined the holotype specimens of *T. buettneri* Case and *T. jacobsi* Murry and made comparisons with other fossils described by Gregory (1945) and in the NMMNH collections from Gregory's localities. Scanning electron microscopy (SEM) work was accomplished on a JEOL-JSM5800 housed at the Institute of Meteoritics at the University of New Mexico Department of Earth and Planetary Sciences. Digital macrophotography was conducted using both a Nikon Coolpix 995 and a Minolta F100. Images were manipulated on a Macintosh G4 computer using Adobe PhotoShop Elements 2.0, and sketches were constructed by tracing digital images in Adobe Illustrator 9.0.

Institutional abbreviations. MNA, Museum of Northern Arizona, Flagstaff; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; TMM, Texas Memorial Museum, Austin; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

HISTORY OF STUDY

Case (1928*a*, *b*) first described fragmentary remains, to which he attributed the new name *Trilophosaurus buettneri* Case, 1928*a*, noting the particularly diagnostic, transversely expanded, lobed teeth with three prominent cusps on the holotype mandible fragment. This specimen is from the Tecovas Formation near Walker's Tank, in Crosby County, West Texas (Text-fig. 1).

From 1939 to 1941, parties working for the US Works Progress Administration (WPA) excavated several paucispecific localities (*Trilophosaurus* quarries 1, 2, 3 and 3A) yielding abundant fossils of *T. buettneri* from the Colorado City Formation of the Chinle Group near Otis Chalk, Howard County, Texas (Lucas *et al.* 1993). Gregory

(1945) published a monograph on the osteology of *Trilophosaurus* based on these fossils, noting two size classes but preferring to maintain all of them in the species *T. buettneri*. The type specimen of *T. buettneri* illustrated by Case (1928*a*, *b*) is clearly of the smaller size class.

Parks (1969) wrote a thesis on the skull and dentition of *Trilophosaurus*, based primarily on the Otis Chalk material. Elder (1978, 1987) studied the taphonomy of the WPA quarries, emphasizing the size differential between the samples of quarries 1 and 3 (larger individuals) and 2 and 3A (smaller individuals), but refraining from assigning taxonomic significance to this size difference. DeMar and Bolt (1981) described the tooth replacement of *Trilophosaurus*, again utilizing the sample from Otis Chalk. Murry (1982, 1986) characterized isolated remains, and later (Murry 1987) named a second species of *Trilophosaurus*, *T. jacobsi*, for isolated tooth and jaw fragments collected from low in the Chinle Group in east-central Arizona (Text-fig. 1). Murry (1989) identified a single occurrence of *T. buettneri* from high in the Blue Mesa Member of the Petrified Forest Formation, and it is included in Long and Murry's (1995) list of specimens referred to *Trilophosaurus*. Later, Sues and Olsen (1993) identified *T. jacobsi* as a probable procolophonid, and proposed the genus name *Chinleogomphius* for the taxon. Long and Murry (1995) concurred, and re-assigned fossils of *Trilophosaurus jacobsi* to '*Chinleogomphius*' *jacobsi*.

Long and Murry (1995) documented several other referred specimens of *Trilophosaurus* sp., based on postcranial bones, from Arizona, New Mexico and Texas. All of the Arizona specimens are either from the *Placerias* quarry, stratigraphically low in the Bluewater Creek Formation (Lucas *et al.* 1997) or are extremely fragmentary material found higher in the stratigraphical section. Presently, none of these specimens is identifiable to species, so we concur with Long and Murry's (1995) assignment of these fossils to *Trilophosaurus* sp. Interestingly, Murry (1986) and Long and Murry (1995) only identified the WPA specimens and other trilophosaurs *sensu stricto* as *Trilophosaurus* sp.

Omitted from Long and Murry's (1995) compendium were occurrences of *Trilophosaurus* documented by Kirby (1989, 1990, 1991, 1993). Kirby identified *Trilophosaurus* from the Owl Rock Formation near Wards Terrace in north-central Arizona. These records were based on an isolated tooth and several fragmentary skull bones discussed below.

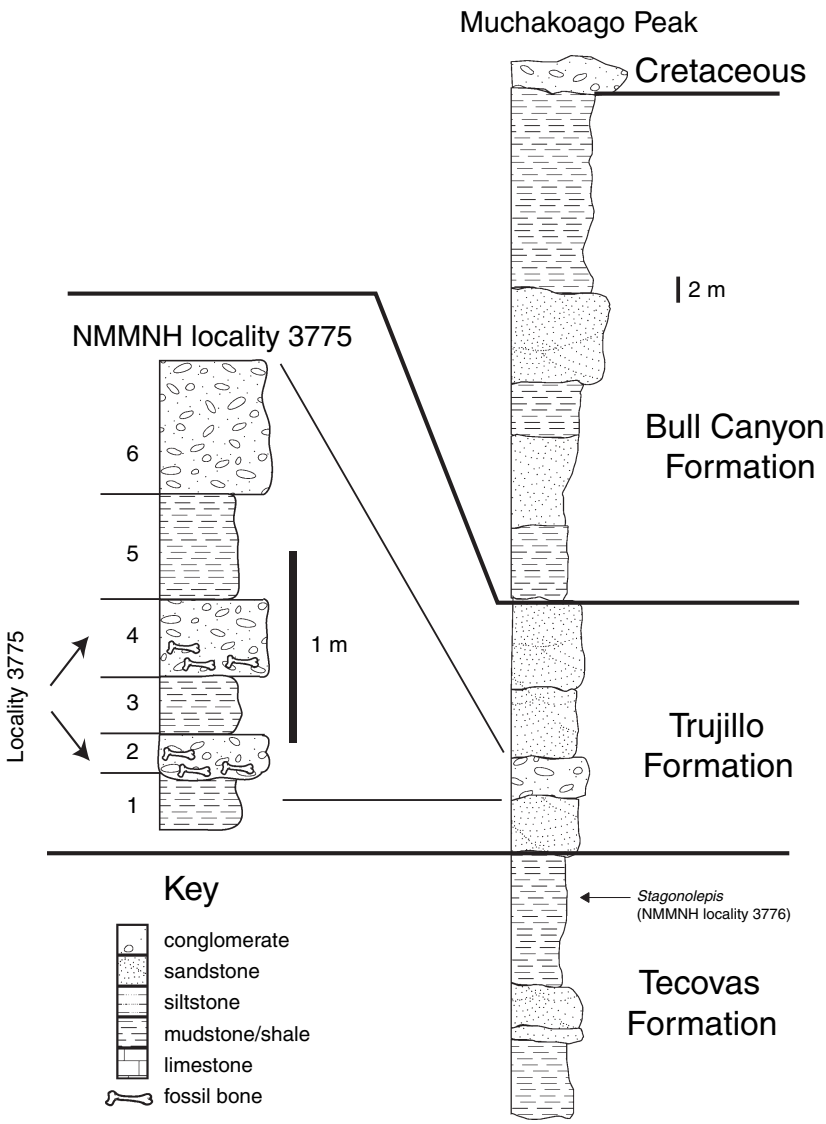
Meanwhile, Lucas *et al.* (1993) documented the stratigraphical and geographical distribution of *Trilophosaurus* in West Texas, based largely on fossils in the private collection of Kahle from the WPA quarries that are now reposited at the NMMNH. Kaye and Padian (1994) acknowledged Murry's (1987) work in their description of the microvertebrate fauna of the *Placerias* quarry (originally studied by Kaye as Tannenbaum 1983), but did not otherwise evaluate the occurrence of *Trilophosaurus* there. Polcyn *et al.* (2002) reported, but did not illustrate, specimens of *T. jacobsi* from strata of the Blue Mesa Member of the Petrified Forest Formation (Chinle Group) near North Stinking Springs Mountain in Arizona (Text-fig. 1). In 2001, we (Heckert *et al.* 2001) provided a preliminary report on the *Trilophosaurus* fossils from the locality that we document here.

STRATIGRAPHY AND AGE

One of us (RK) discovered NMMNH locality 3775 while working in West Texas in the early 1990s (Text-figs 1–2). Heckert *et al.* (2001) published a preliminary review of the geology and fauna of this site, and we expand upon their observations here. This locality yields numerous pinkish-grey disarticulated bones from a matrix of intraformational conglomerate. The principal fossiliferous horizon consists of a moderate brown, clast-supported conglomerate of rounded, flattened, intraformational mud pebbles up to 2 cm in diameter. The matrix is principally a rounded, moderately poorly sorted sublitharenite. This horizon is separated from the underlying moderate brown mudstone along an irregular contact that suggests slight scouring and erosion (Text-fig. 2). Most of the overlying strata are interbedded sandstone, conglomerate and mudstone. Unionid bivalves were collected from the uppermost conglomerate, which is a moderate yellowish-brown intraformational conglomerate dominated by clasts of calcrete and siltstone up to 1·5 cm in diameter.

The bedded intraformational conglomerates that dominate this outcrop strongly resemble the dominant lithologies of the Trujillo Formation of the Chinle Group (Lucas *et al.* 1994, 2001). However, the possibility exists that these strata instead represent an outcrop of the more areally limited coarse-grained channel bodies within the stratigraphically lower Tecovas Formation (Lucas *et al.* 1994 and sources cited therein). Because these are some of the only outcrops in an area characterized by broad flatlands, there is some uncertainty as to the exact stratigraphical position of these strata. However, we conclude that these deposits represent the base of the Trujillo Formation locally, and summarize arguments both for and against that assignment in the following paragraphs.

Trujillo Formation strata overlie a regional erosional surface termed the Tr-4 unconformity by Lucas (1993) that approximates the Carnian/Norian boundary as defined in the terrestrial realm (Lucas 1998). Although exposure in the vicinity of NMMNH locality 3775 is poor, strata to the north and west clearly pertain to the Bull Canyon Formation, which overlies the Trujillo Formation throughout West Texas and east-central New



TEXT-FIG. 2. Stratigraphical columns of Triassic strata in Borden County, West Texas, showing the position of NMMNH localities 3775 and 3776.

Mexico. Similarly, the Trujillo Formation throughout this region is considerably more resistant than either the overlying Bull Canyon Formation or the underlying Tecovas Formation. Thus, the Trujillo Formation crops out as either a ledge-former above Tecovas Formation badlands, such as at Muchakoago Peak slightly to the south-east or, alternatively, as a bench flooring broad plains beneath localized exposures and badlands of the Bull Canyon Formation. The strata at NMMNH locality 3775 appear to represent the latter, as they are part of a broad upland surface that extends from Gail to the north-east, and southward to just north-west of Westbrook.

NMMNH locality 3775 is in an outcrop of interbedded mudstone and intrabasinal (mostly calcrete and mudstone pebble rip-up) conglomerate, a characteristic lithotype of the Trujillo Formation in West Texas (e.g. Gould 1907; Lucas and Anderson 1993; Lucas *et al.* 2001). Indeed, the locality, just west-south-west of Gail in western Borden County, is at the base of a dissected surface underlain by the Trujillo Formation that can be traced due east on strike to Muchakoago (also called 'Mushaway' on some maps) Peak, about 21 km from NMMNH locality 3775 (Text-fig. 2).

At Muchakoago Peak, an approximately 75-m-thick Chinle Group section is exposed, and has been described by various workers, including Drake (1892) and Finch and Wright (1983) (Text-fig. 2). They described this section as including a medial interval of sandstone and intrabasinal conglomerate termed 'central beds' by Drake (1892, pl. 5) and subsequently assigned to the Trujillo Formation of Gould (1907) by Reeside *et al.* (1957) and Finch and Wright (1983), among others. Underlying mudstones thus are assigned to the Tecovas Formation (e.g. Finch and Wright 1983), and overlying mudstones

are termed Bull Canyon Formation (e.g. Lucas *et al.* 1994, 2001). The Trujillo Formation interval at Muchakoago Peak is the same sandstone/conglomerate interval that encompasses NMMNH locality 3775 to the west. Furthermore, at NMMNH locality 3776, about 9 km south-west of Muchakoago Peak, the Adamanian index aetosaur *Stagonolepis* occurs in the mudstone-dominated interval below the strata we identify as Trujillo. This occurrence supports assigning these mudstone-dominated strata to the Tecovas Formation, as that unit is of Adamanian age elsewhere (e.g. Lucas *et al.* 1994, 2001), and indeed includes the type locality of the aetosaur *Stagonolepis wellesi* (Long and Ballew 1985; Heckert and Lucas 2002).

Identification of the fossiliferous strata at NMMNH locality 3775 as Trujillo Formation thus is consistent with previous interpretations of Upper Triassic stratigraphy in Borden County, Texas. An exception is Lehman (1994), who mapped all Triassic strata in Borden County as Bull Canyon Formation (his 'Cooper Canyon Formation'). Lucas *et al.* (1994), nevertheless, presented a detailed refutation of Lehman's (1994) mapping, which is also inconsistent with previous work on Upper Triassic stratigraphy cited here as well as regional geological maps prepared by McKee *et al.* (1957).

The only other possibility is that these strata represent a channel deposit in the Tecovas Formation, which typically consists of variegated mudstones we interpret as floodplain deposits, with discontinuous, lenticular, coarser-grained channel bodies. However, we note here that the broad flats of which this outcrop is a part suggest that the rocks flooring these flatlands are not composed of isolated channel-fill lithologies, and instead represent more regional deposition of coarse-grained strata. Therefore, we assign NMMNH locality 3775 to the Trujillo Formation.

These strata are probably at or near the Carnian/Norian boundary as typically interpreted in the terrestrial realm. However, we follow Lucas (1998) and note the extreme difficulty of correlating non-marine tetrapod occurrences to a marine timescale. Instead we use his system of land-vertebrate faunachrons (LVF) to denote the age of non-marine Upper Triassic strata. Accordingly, the Tecovas Formation is of well-established Adamanian (latest Carnian) age, based on the occurrence of the Adamanian index taxa *Rutiodon* (= *Leptosuchus*) and *Stagonolepis* (Lucas and Hunt 1993; Lucas *et al.* 1994). The Trujillo Formation is slightly younger. Tetrapod fossils, including the occurrence of *Typothorax coccinarum* (Hunt 2001; Lucas *et al.* 2001), suggest that the Trujillo is of Revueltian (early mid Norian) age, although palynological evidence indicates that the basal Trujillo could be as old as latest Carnian (Dunay and Fisher 1974, 1979; Litwin *et al.* 1991; Cornet 1993). Because NMMNH locality 3775 lies above the lowest stratigraphical occurrence of *Stagonolepis* and *Rutiodon* but below the lowest occurrence of *Typothorax coccinarum* (at least locally), we consider it to be latest Adamanian in age.

PALAEONTOLOGY

We have collected numerous macro- and microvertebrate fossils from NMMNH locality 3775. Although many of these fossils have yet to be prepared, it is evident that this locality yields several tetrapod taxa, dominated (> 95 per cent) by fossils of the archosauromorph reptile *Trilophosaurus* (Heckert *et al.* 2001). The associated fauna includes indeterminate coprolites, unionid bivalves, osteichthyans, indeterminate reptiles, fragmentary phytosaurs, a possible ornithischian dinosaur, and probable theropods, including an unusual archosaur with elongate neural spines superficially similar to those of the putative theropod dinosaur *Spinosuchus caseanus* Huene (Heckert *et al.* 2001). Most of this fauna was described previously (Heckert *et al.* 2001) or will be treated separately elsewhere. This paper focuses on the occurrence of *T. jacobsi* at this locality.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Laurenti, 1768
Subclass DIAPSIDA Osborn, 1903
Superorder ARCHOSAUROMORPHA Huene, 1946
Family TRILOPHOSAURIDAE Gregory, 1945

Genus TRILOPHOSAURUS Case, 1928*a*

1993 *Chinleogomphius* Sues and Olsen, 1993

Type species. Trilophosaurus buettneri Case, 1928*a*, from the Upper Triassic of Texas, USA.

Trilophosaurus buettneri Case, 1928*a*
Text-figures 3, 7B, D, F, H

1928*a* *Trilophosaurus buettneri* Case, p. 177, fig. 1.
1928*b* *Trilophosaurus buettneri*; Case, p.1, pl. 1, figs 1–5.
1945 *Trilophosaurus buettneri*; Gregory, p. 273, figs 2–11, pls 19–33, 8 unnumbered tables.
1956 *Trilophosaurus buettneri*; Romer, p. 165, figs 88, 110c, 121i, 140t–u, 147b, 158b, 186d, 189f.
1966 *Trilophosaurus buettneri*; Romer, p. 122, figs 181, 182.
1969 *Trilophosaurus buettneri*; Parks, p. 1, figs 1–22, 24–39.
1969 *Trilophosaurus buettneri*; Kuhn, p. 24, pl. 11, fig. 1; pl. 12, figs 6, 12.
1969 *Trilophosaurus*; Kuhn, p. 24, pl. 12, figs 1–4.

1981 *Trilophosaurus buettneri*; DeMar and Bolt, p. 967, figs 1, 4–5, 6?, 7–8.
1986 *Trilophosaurus buettneri*; Murry, p. 116, fig. 9.5G–G2, 9.13a.
1988 *Trilophosaurus buettneri*; Carroll, p. 264, figs 13-2c, 13-3d, 13-6.
1989 *Trilophosaurus buettneri*; Murry, p. 249, fig. 7h.
1993 *Trilophosaurus buettneri*; Lucas *et al.*, p. 237, fig. 4a–i.
1997 *Trilophosaurus*; Benton, p. 144, fig. 6.5a–b.
2004 *Trilophosaurus buettneri*; Heckert, p. 1, figs 37, 76.

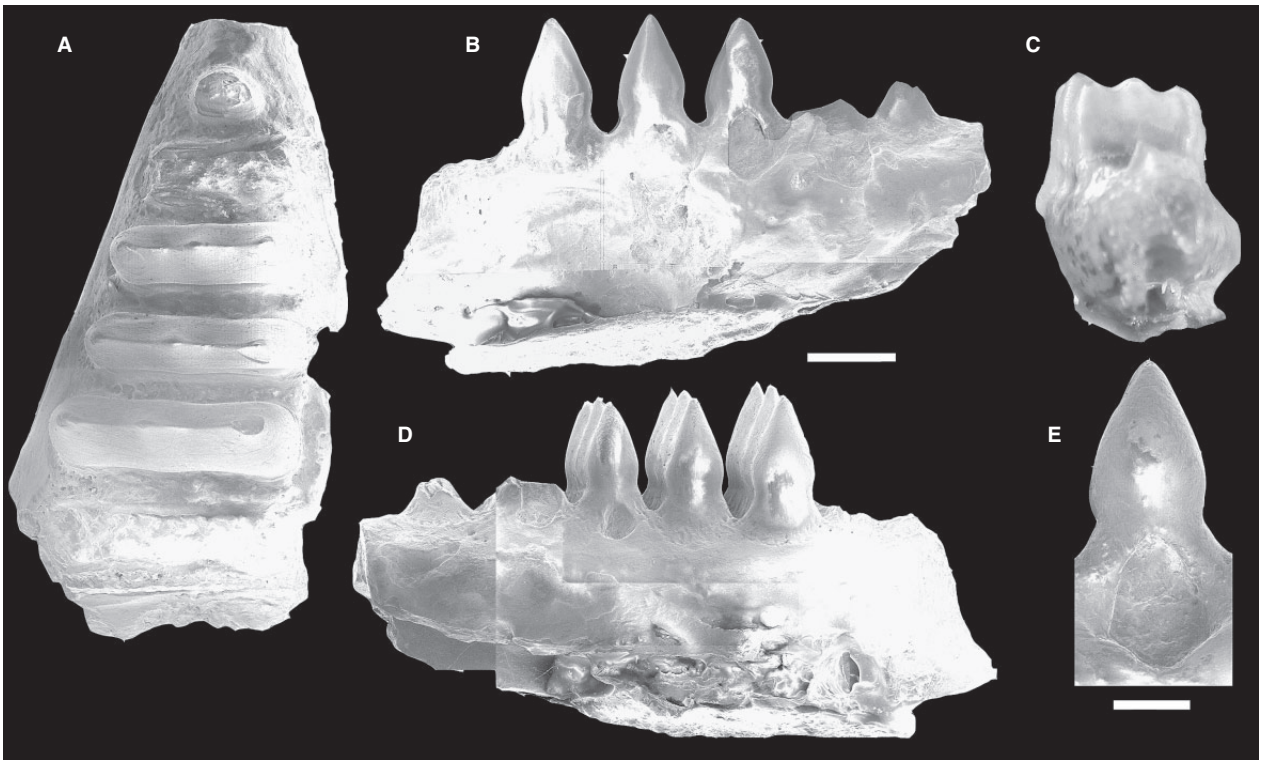
Holotype. UMMP 2338, an incomplete right dentary fragment bearing parts of five teeth from the Tecovas Formation near Walker's Tank, Texas, USA (Text-fig. 3).

Referred material. Known fossils of *T. buettneri* include (but are not necessarily limited to) the fossils listed by Long and Murry (1995) in their appendix. Key specimens include the holotype, the TMM specimens from *Trilophosaurus* quarries 1, 2, 3 and 3A, and microvertebrate specimens described from several localities by Heckert (2001, 2004), which include NMMNH P-34291 from locality 1312.

Revised diagnosis. A species of *Trilophosaurus* distinguished from *T. jacobsi* by the lack of prominent cingula linking the cusps both labiolingually across the centre of the tooth and also along the mesial and distal margins of the tooth; central cusp subequal in height to the labial and lingual cusp; central cusp not displaced labially or lingually, so tooth crown is labiolingually symmetrical in occlusal view.

Redescription. The holotype, UMMP 2338, is an incomplete right dentary bearing parts of five teeth and six total tooth positions. As preserved the specimen is 17 mm long, approximately 6·7 mm at the widest point, and tapers to 2·5 mm wide anteriorly. Throughout the tooth row the implantation appears to be ankylothecodont. All of the teeth are ankylosed to the bone, but broken teeth indicate that substantial roots were present below the bone surface. Indeed, in either lateral or lingual view it is apparent that there was a substantial gap between the base of the crown and the actual root surface (Text-fig. 3).

The lingual margins of all teeth are aligned in a straight line anteroposteriorly relative to the rest of the jaw (mesiodistally relative to tooth crowns). Broader teeth extend further on the labial side than teeth that are less wide. There are foramina lingual to teeth 2, 3 and 4, and labial to tooth 3. On all preserved teeth the cusps are transversely aligned and evenly spaced. The lingual and labial cusps are always near, but not quite at, the margin of the tooth. Thin ridges (cingula) run transversely across the centre of the tooth crown connecting the central cusp to each of the marginal cusps. There are no other cingula. Unlike procolophonids, the areas between the cusps are not hollowed out or deeply concave.



TEXT-FIG. 3. Scanning electron micrographs of UMMP 2339, holotype right dentary of *Trilophosaurus buettneri* Case (UMMP 2338) in A, occlusal, B, labial, C, anterior, and D, lingual views. E, close-up view of third tooth position of same in labial view. Scale bar represents 2 mm in A–D and 1 mm in E.

The first tooth is relatively complete. In occlusal view, this tooth is somewhat triangular with a blunt apex mesially and rounded corners on the labial and lingual edges of the distal margin. The tooth was probably low and blunt, without accessory cusps. The enamel is broken in many places, exposing the dentine and, possibly, the central pulp cavity.

The second tooth is broken off below the crown, but the preserved roots demonstrate that it was very wide transversely. This tooth was probably the anteriormost tricuspid tooth, but the third tooth is the anteriormost of the three well-preserved tooth crowns.

There are three well-preserved, tricuspid teeth, in tooth positions 3, 4 and 5. In all of these teeth the crowns are approximately 1·5 mm long, and the labial and lingual cusps are usually *c.* 1·5 mm from the central cusp. These teeth are 3·7, 4·3 and 4·8 mm wide, respectively. On all preserved teeth the cusps are transversely aligned and evenly spaced.

Remarks. Prior to the work of Murry (1982, 1986, 1987), all reptiles with transversely broad, tricuspate teeth from the Upper Triassic of the south-western USA were referred to *T. buettneri* Case, and indeed Gregory (1945) made little comment on the extremely incomplete nature of the type specimen of *T. buettneri*. Murry (1987) chose what he thought was a homologous element, a 'right dentary', for the type specimen of *T. jacobsi*, facilitating comparison of the two taxa. Two important conclusions of this study are that (1) the holotype of *T. jacobsi* is an incomplete left maxilla, not a right dentary fragment (see section on *T. jacobsi*, below); and (2) we do not think that the size difference has taxonomic significance, because we consider the holotype of *T. buettneri* to represent a juvenile individual (and, by extension, the holotype of *T. jacobsi* to represent a hatchling individual).

Trilophosaurus jacobsi Murry, 1987
Text-figs 4–6, 7A, C, E, G

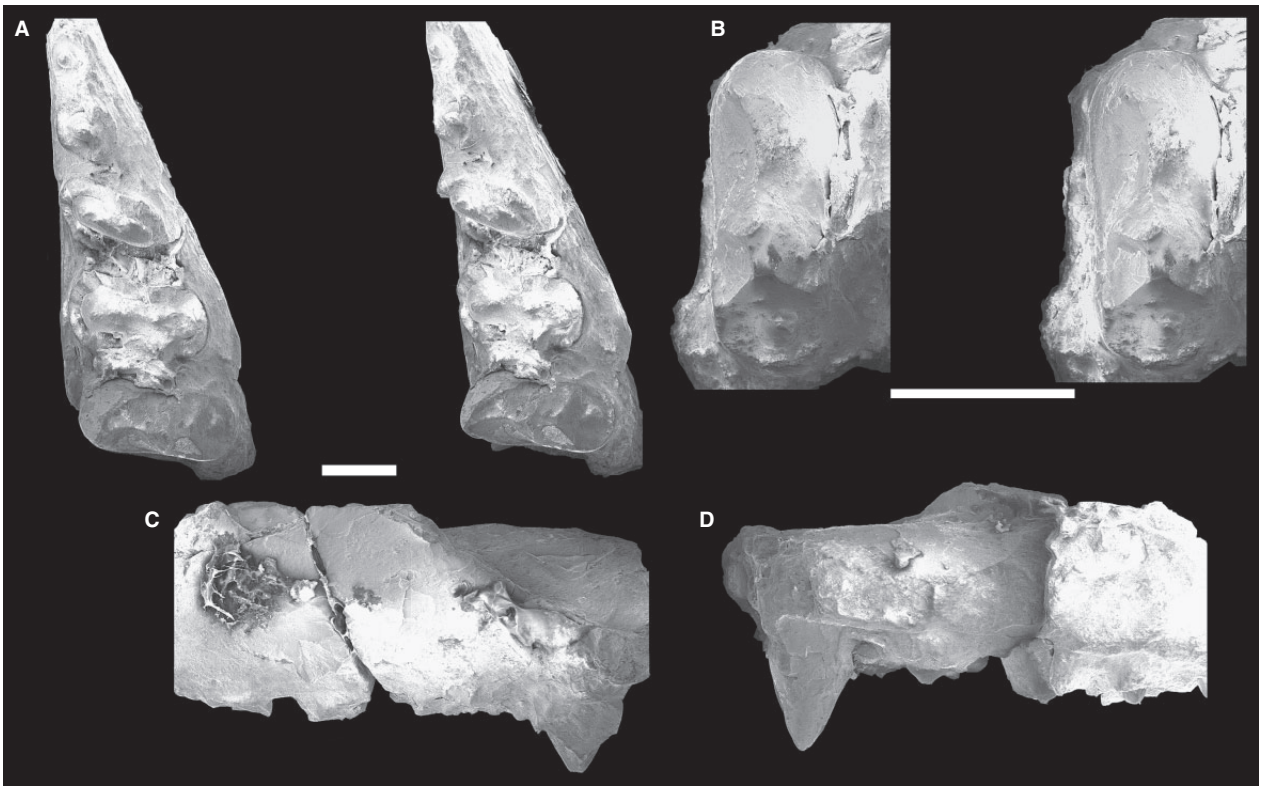
1987 *Trilophosaurus jacobsi* Murry, p. 773, figs 1–3.
1993 *Chinleogomphius jacobsi* Sues and Olsen, p. 285.
2001 *Trilophosaurus* sp.; Heckert *et al.*, p. 115, fig. 2a–e.
2001 *Trilophosaurus buettneri*; Heckert *et al.*, p. 118, fig. 3a.
2004 *Trilophosaurus jacobsi*; Heckert, p. 1, figs 77, 100.

Holotype. MNA V3192, a tooth-bearing left maxilla fragment from the *Placerias* quarry, Upper Triassic Bluewater Creek Formation of Arizona, USA (Text-fig. 4).

Referred specimens. Murry (1987) referred what he considered three dentary fragments (MNA V3193, V3198 and V3199), two maxillary fragments (MNA V3194, V3197) and, tentatively, two isolated teeth (MNA V3195, V3200), to *T. jacobsi*. We have re-examined these specimens and reject Murry's (1987) assignment of MNA V3195 and V3200 to *Trilophosaurus* and instead consider them teeth of ornithischian dinosaurs (see below). The other specimens (MNA V3193–V3194, V3197–V3199) are topotypes of *T. jacobsi*. Table 1 summarizes our interpretation of the original MNA specimens. Because Murry (1987) provided little description of these specimens individually and did not photographically illustrate any of them, we illustrate and re-describe them here in addition to providing the first photographic illustrations of the holotype. Additionally, we illustrate and describe topotype specimens (MNA V9494, Text-fig. 5K–L; V9495, Text-fig. 5M) and refer specimens of '*Chinleogomphius*' *jacobsi* (*sensu* Heckert 2001) and the *Trilophosaurus* specimens described by Heckert *et al.* (2001) to *T. jacobsi*. The latter include NMMNH P-34073, tooth and P-34372, tooth fragment (Heckert 2001, fig. 5.11E–F) from NMMNH locality 1430, NMMNH P-34447, tooth fragment, P-34448, tooth fragment, and P-34472, incomplete tooth from NMMNH locality 2739 (see also Heckert 2004). These latter specimens are described later in this paper in the section on biostratigraphy. Many are not diagnostic to species, but given that *T. jacobsi* is the only known species from that locality, it appears likely that all such specimens pertain to *T. jacobsi*.

Revised diagnosis. Trilophosaurus species distinguished from all other trilophosaurids (and similar taxa) except *T. buettneri* by the presence of a dental battery of transversely broadened, ovate, unconstricted tricuspate teeth; distinguished from *T. buettneri* by the presence of prominent cingula linking the cusps both labiolingually across the centre of the tooth and also along the mesial and distal margins of the tooth; the tooth is asymmetrical in occlusal view, with the central cusp offset labially; the central cusp is the tallest cusp, and is asymmetric in occlusal view with a rounded, convex lingual margin and a more complex, steeper-sided, doubly concave labial margin; sometimes the tip of this cusp is worn so that it is roughly pentagonal in occlusal view. The lingual cusp is low, transversely expanded, and mesiodistally compressed. The labial cusp has 3–4 denticles on newly erupted teeth that rapidly wear to create a smooth transverse cusp. Murry (1987) already provided detailed descriptions separating teeth of *Trilophosaurus* from most other grossly similar multicuspid teeth of other tetrapod taxa, and we generally agree with his descriptions. We note also that *T. jacobsi* differs from *Variodens* and *Tricuspisaurus* in having a central cusp markedly taller (*c.* 20 per cent) than the marginal cusps.

Redescription of holotype. The holotype of *T. jacobsi* (Text-fig. 4) is a *c.* 6-mm-long fragment of bone that Murry (1987) interpreted as a right dentary that was broken anteriorly and posteriorly. We interpret the bone as a left maxilla broken anteriorly, posteriorly and dorsally. Five tooth positions are preserved, but only one (the fifth) contains a relatively well-preserved tooth. The first tooth appears to have been small and nearly circular in cross-section with a diameter of *c.* 0·2 mm. The second tooth is somewhat larger (diameter *c.* 0·3–0·4 mm) but similarly simple, albeit more ovate in occlusal cross-section. The third tooth position bears the first



TEXT-FIG. 4. Scanning electron micrographs of the holotype of *Trilophosaurus jacobsi*, Murry (MNA V3192). A, C–D holotype left maxilla(?) in A, stereo occlusal, C, labial, and D, lingual views. B, stereo occlusal view of penultimate preserved tooth. Scale bars represent 1 mm.

transversely broadened tooth, although the tooth itself is broken, so nothing can be said about the size, shape and distribution of cusps, cingula or other features of the crown. Based on the preserved root and base, this tooth was probably *c.* 1 mm wide and 0·3 mm long. The fourth tooth is also basically destroyed, but appears to be similarly wide and slightly longer. The fifth tooth position bears the only well-preserved tooth. This crown is the widest yet (*c.* 1·5 mm) but appears to be no longer than was the fourth tooth. The tooth preserves three cusps, with the central cusp taller than either the labial or the lingual cusp. The central cusp is strongly offset toward the labial margin, so that the lingual margin of the cusp is near the centre of the tooth, with the rest of the cusp labial to this point. Both the labial and the lingual cusps are comparatively low, and connected to the central cusp both by a transverse cingulum and by mesial and distal cingula. The central cusp is strongly faceted, so that the worn tip is pentagonal in occlusal view. The combination of labial offset and faceting of the central cusp gives it an asymmetrical pyramidal shape, with a steeper labial margin and more gentle mesial-lingual and distal-lingual slopes. The cingula bounding the facets extend basally to the mesial and distal cingula. This tooth morphology is, as previous authors have noted, more complex than that of *T. buettneri*. In the following paragraphs we describe the rest of the type series as well as fossils with a similar dentition that we assign to *T. jacobsi* and that give us the first detailed insight into the craniomandibular and dental anatomy of the species.

Redescription of topotype specimens. Murry (1987) referred five tooth-bearing fragments and, tentatively, two teeth, all from the *Placerias* quarry, to *T. jacobsi* (Table 1). Of these specimens, we remove the two teeth, MNA V3195 (Murry 1987, fig. 4) and V3200 (unfigured referred specimen), from *T. jacobsi*, tentatively referring them instead to the putative ornithischian taxon *Revueltosaurus hunti* Heckert, 2002 (compare Heckert 2002, figs 5–7 with Murry 1987, fig. 4). The other specimens we consider to be topotypes as they are from the same locality as the holotype. Here we redescribe and provide the first photographic illustrations of these five tooth-bearing fragments (Text-fig. 5A–J). We also illustrate and describe isolated teeth that are topotypes and that were not available to Murry (Text-fig. 5K–M).

Description of topotype maxillary fragments. Topotype specimen MNA V3194 (Text-fig. 5A) is an anteriorly tapering bone fragment identified as a mandible and illustrated by Murry (1987, fig. 2). We interpret this specimen as a right maxilla fragment. The anterior margin is broken across a tooth socket that probably represents either the second or the third tooth position. Posterior to this is a multicuspid tooth that is probably the first or second tricuspate tooth. It is approximately 0·7 mm long and 1 mm wide, with a broken labial(?) cusp.

TABLE 1. Redesignation of type material of *Trilophosaurus jacobsi* Murry.

Specimen	Murry (1987) interpretation	This paper
MNA V3192	Holotype right mandible (Murry 1987, fig. 1)	Holotype left maxilla fragment (Text-fig. 4)
MNA V3193	(Topotype) mandible fragment	Topotype left dentary fragment (Text-fig. 5F–G)
MNA V3194	(Topotype) maxilla fragment (Murry 1987, fig. 2)	Topotype right maxilla fragment (Text-fig. 5A)
MNA V3195	(Topotype?) tooth (Murry 1987, fig. 4)	Tooth of *Revueltosaurus hunti*
MNA V3197	(Topotype) maxilla fragment (Murry 1987, fig. 3)	Topotype right maxilla fragment (Text-fig. 5B)
MNA V3198	(Topotype) mandible fragment	Topotype posterior right maxilla fragment (Text-fig. 5C–E)
MNA V3199	(Topotype) mandible fragment	Topotype left dentary fragment (Text-fig. 5H–J).
MNA V3200	(Topotype?) tooth	Tooth of *Revueltosaurus hunti*

Enough of the crown is preserved to show the asymmetrical central cusp we consider to be diagnostic of *T. jacobsi*, and the tooth bears mesial and distal cingula as well. The next tooth is larger (still 0·7 mm long but *c.* 1·2 mm wide) and somewhat better preserved. All three cusps are connected by cingula, including a transverse cingulum and mesial and distal cingula. The central cusp is offset lingually and is asymmetrical, as described in the previous specimen.

We also interpret MNA V3197 (Text-fig. 5B) as a right maxilla fragment. This specimen is extremely small, broken across tooth sockets both anteriorly and posteriorly, and only preserves a single tricuspate tooth measuring *c.* 0·6 mm long and 1·1 mm wide. The tooth is asymmetrical in occlusal view, with a labially offset central cusp. All three cusps are connected by a transverse cingulum and mesial and distal cingula. The central cusp is faceted and asymmetrical, with the shorter base lingual and more elongate sides on the labial surfaces.

Another topotype right maxilla fragment, MNA V3198 (Text-fig. 5C–E) is a tooth-bearing bone fragment that is extremely similar to MNA V3197 but represents a different quadrant of the jaw, either the opposite side or else the occluding counterpart. Like MNA V3197 the bone is broken across each of two sockets with a single tooth preserved between the breaks. Because the sockets increase in size along the specimen, we suspect that these correspond with tooth positions 3–5. The single preserved tooth is transversely broadened (*c.* 0·5 mm long by 1·2 mm wide) and tricuspate, with all three cups connected by both the transverse cingulum and the mesial and distal cingula.

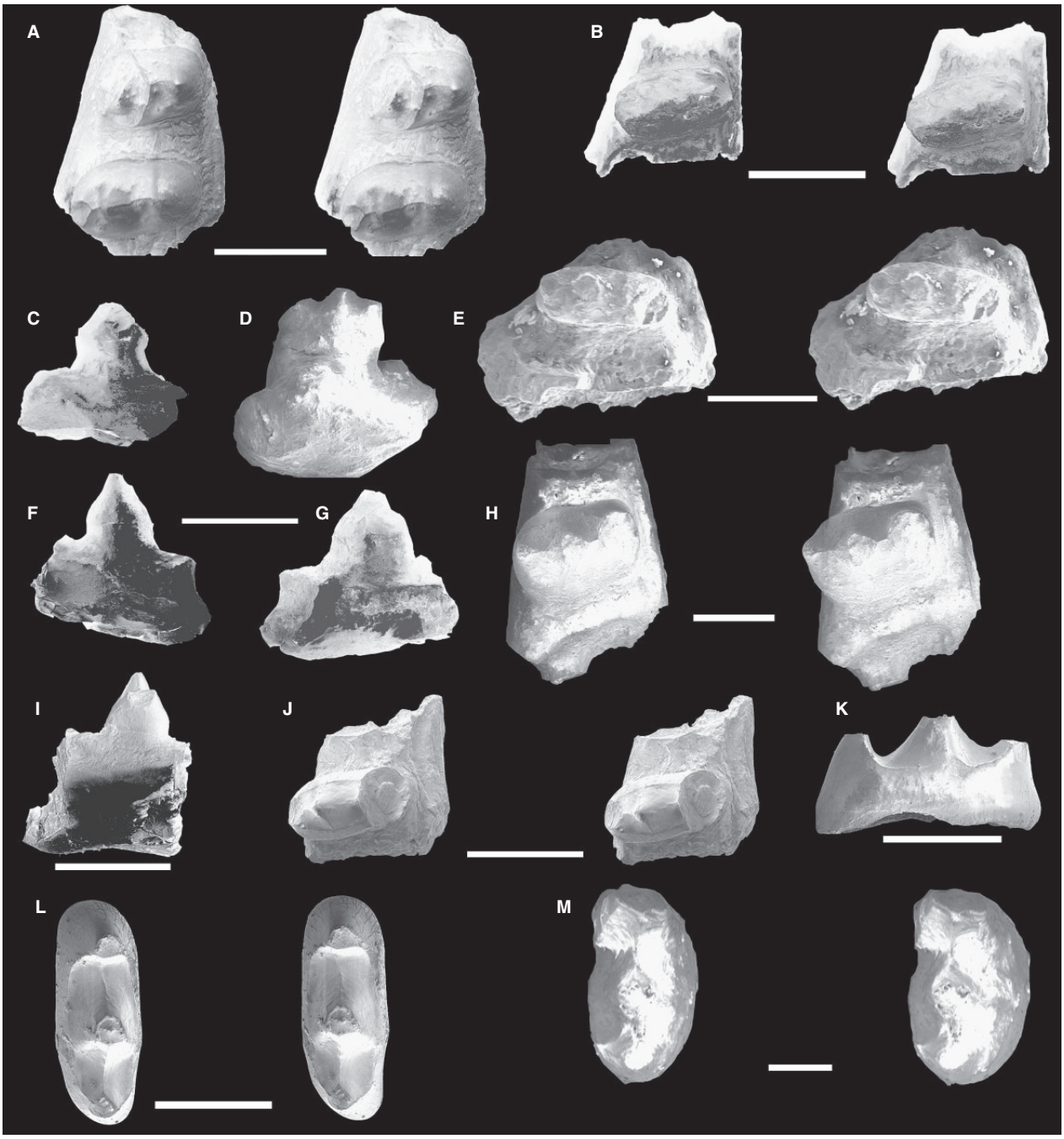
Description of topotype dentary fragments. Topotype dentary fragments include MNA V3193 and V3199. MNA V3193 (Text-fig. 5F–H) is a left dentary fragment that tapers anteriorly and bears a single tricuspate tooth, although the labial cusp is broken. The remnants of tooth sockets anterior and posterior to this tooth crown indicate that it is probably the fourth overall in the series. It is significantly wider than the socket anterior to it, but the anterior socket is still much broader than wide, and probably bore a tricuspate tooth in life. The posterior socket is wider still, so in this respect the fragment matches closely the holotype of *T. jacobsi*. The single preserved tooth appears to be strongly ankylosed to the bone. It is relatively narrow, *c.* 0·7 mm wide labiolingually by 1·0 mm long mesiodistally. Each of the three cusps is connected by a single transverse cingulum and two marginal cingula. The central cusp is very slightly taller than the marginal cusps and slightly offset lingually. The central cusp is asymmetrical in occlusal view, being pentagonal in cross-section, with the base of the pentagon on the most lingual surface, shorter facets distally and mesially on the next-most labial faces, and two longer facets on the labial-most faces, forming the typical *T. jacobsi* cusp.

We interpret MNA V3199 (Text-fig. 5I–J) as another topotype left dentary fragment. This tooth fragment bears a well-preserved tooth lacking only a single marginal cusp. We suspect that this tooth occupied a relatively anterior position in the jaw. The tooth is firmly ankylosed to the jaw and indeed has a low profile in labial or lingual view. It is clearly tricuspate with an offset central cusp. The cusps are all connected by a transverse cingulum as well as mesial and distal cingula. The central cusp is offset labially.

Description of topotype teeth. One of the topotypes, MNA V9494, is a particularly well-preserved, apparently shed, tricuspate tooth (Text-fig. 5K–L). The tooth is relatively large and proportionately wide (1·9 mm wide by 0·7 mm long), and complete except for minor breakage (wear?) at or near the apex of each cusp. The central cusp is offset, and all three cusps are connected by transverse, mesial and distal cingula. Although worn and/or damaged, the central cusp was clearly the tallest of the three, and is also faceted asymmetrically in the manner described above for *T. jacobsi* teeth found in bone fragments. We consider this tooth to be more worn than broken, indicating at least some cusp-to-cusp occlusion in *T. jacobsi*.

Another shed topotype tooth, MNA V9495, is probably one of the anteriormost teeth in the *T. jacobsi* dentition and the smallest tooth described here (Text-fig. 5M). It is proportionately much less wide (*c.* 0·4 mm wide by 0·6 mm long). Consequently, the central cusp is only slightly offset labially. Like the other teeth described here, this tooth bears transverse, mesial and distal cingula connecting all three cusps. The central cusp is faceted, with shorter facets on the labial side and longer facets lingually.

Description of referred specimens. Here we describe the first reasonably complete skull and mandible of *T. jacobsi*, NMMNH P-41400 (Text-fig. 6). In so doing, we note the extreme difficulty previous authors have experienced in discerning sutural relationships of *Trilophosaurus buettneri*. Indeed, in Gregory's (1945) reconstruction, incorporated into classic texts by Romer (1956) and Carroll (1988), essentially no sutures are delineated. Parks (1969) re-studied the WPA samples and superimposed sutures for many skull bones on Gregory's (1945) plates. Merck (1995) presented preliminary evidence that computer-aided tomography (CAT-scan) had provided new insights into the cranial anatomy



TEXT-FIG. 5. Scanning electron micrographs of topotype specimens of *Trilophosaurus jacobsi* Murry from the *Placerias* quarry (Bluewater Creek Formation: Adamanian, Apache County, Arizona, USA). A, MNA V3194, topotype right maxilla fragment in stereo occlusal view. B, MNA V3197, topotype right maxilla fragment in stereo occlusal view. C–E, MNA V3198, topotype right maxilla fragment in C, lateral, D, anterior, and E, stereo occlusal views. F–H, MNA V3193, topotype left dentary fragment in F, lateral, G, medial, and H stereo occlusal views. I–J. V3199, topotype left dentary fragment in I, labial, and J, stereo occlusal views. K–L, MNA V9494, topotype tooth in K, anteroposterior and L, stereo occlusal views. M, MNA V9495, topotype tooth in stereo occlusal view. Scale bars represent 1 mm.

of *T. buettneri*, including the fact that many of the sutures have gliding (not abutting) contacts that necessarily change apparent position if bone is worn away from the external surface. Lamentably, this study remains unpublished except in its most preliminary form (Merck 1995). Consequently, the cranial descriptions that follow are based on an amalgamation of our own observations and interpretations of the specimen augmented principally by Parks's (1969) restoration of the skull of *T. buettneri*.

The new specimen of *T. jacobsi* we describe here is an articulated, incomplete skull and mandible. The skull is best preserved on the left side, which includes all of the bones except for most of the premaxilla, part of the anterior maxilla and the quadrate, and the ventral margins of the jugal, the quadratojugal and the quadrate. The right side is much less complete, and lacks part or all of all elements except for portions of the frontal, the postfrontal, the parietal and the squamosal. Although laterally compressed and damaged, NMMNH P-41400 preserves well the left side of the skull in both internal and external views (Text-fig. 6A–D). In overall shape it resembles the skull of *T. buettneri* (Gregory 1945, figs 2–4, pl. 20, fig. 1; Romer 1956, fig. 88), but differs in some key features: (1) the skull roof is not peaked at the lambdoidal crest in *T. jacobsi*, but instead peaks in a broad arc just posterodorsal to the orbit; (2) the relative size of the orbit of *T. jacobsi* is much larger than in *T. buettneri*, although this may be simply due to a difference in ontogenetic age of the specimen we illustrate here relative to specimens illustrated by Gregory (1945); and (3) *T. jacobsi* does not have a single, peaked sagittal crest as in *T. buettneri*, but instead has two separate parasagittal crests offset from the midline on the right and left sides (Text-fig. 6E–F). The last of these could conceivably be an ontogenetic difference, although we consider this to be extremely unlikely as this kind of ontogenetic variation is not present in phylogenetically similar taxa such as rhynchosaurs (Benton 1990), nor is the observed variation in jaw adductor crests on the parietal of *Prolacerta* (Modesto and Sues 2004) attributable to ontogenetic variation.

In lateral view (Text-fig. 6A–B), NMMNH P-41400 lacks almost all of the premaxilla, so the anterior tip of the preserved skull begins at the posterior end of the nasal opening. The rostrum anterior to the orbit is short and tall, and ventral to the orbit there are nine teeth and two alveoli rooted in the maxilla. As in *T. buettneri* (e.g. Parks 1969), separate sutures of the nasals, the maxilla, the prefrontal and the lacrimal cannot be delineated on NMMNH P-41400. However, a clear suture for the jugal with the postorbital is visible just posterior to the ventral edge of the orbit, as is a squamosal-quadrate suture just posterior to the jugal-postorbital suture. The orbit is rather large (maximum diameter, 22 mm; maximum length, 24 mm). Part of the pterygoid and/or ectopterygoid is visible in the medial wall of the orbit. Dorsal and posterior to the orbit, a relatively large (maximum diameter, 19 mm) supratemporal fenestra opens dorsally. In the following paragraphs we describe the observed bones of the skull individually.

Most of the premaxilla is missing, and indeed, we can only infer its presence based on the preserved posterior margin of the external naris, as there are no discernible sutures between the premaxilla and the maxilla or the nasals. The first preserved teeth are clearly in the maxilla, so we infer that, like *T. buettneri*, *T. jacobsi* had an edentulous premaxilla.

The maxilla is the largest preserved skull bone, and appears to occupy most of the skull ventral and anterior to the orbit (Text-fig. 6A–D). The maxilla appears to occupy the bulk of the ventral floor of the orbit, and the maxilla ventral to the orbit has several irregularly arranged nutrient foramina dorsal to the tooth row (Text-fig. 6B). The left maxilla preserves 11 tooth positions, eight of which are occupied by teeth in varied states of preservation (Text-fig. 6G–H). Beginning with tooth 3, all are transversely broad and bear three cusps. Each of the teeth is *c.* 1·5 mm long. These teeth increase in width from *c.* 5·3 to 7·6 mm from tooth positions 3 to 8, before decreasing again to *c.* 5 mm at the end of the tooth row (inferred from the width of the alveolus). The central cusp is the most prominent, and is offset slightly labially from the centre of the tooth. The central cusp is weakly faceted, with two elongate facets on the lingual surface and two shorter facets on the labial side. All of these teeth bear cingula connecting the central cusp to the labial and lingual cusps. They also bear strong cingula distally and mesially. Lingually, the lingual cusp is rimmed by cingula, a feature not reported from *T. jacobsi* previously, that might serve to distinguish maxillary teeth of *T. jacobsi* from dentary teeth (described below). The lingual margins of the teeth are aligned so that the lingual cusps are nearly in a straight line anteroposteriorly. Consequently, the labial margin of the tooth row, as well as the arc formed by the central and labial cusps, is convex.

Only a thin sliver of the posterior portion of the left nasal is preserved, based on our interpretation of a probable lateral suture with the maxilla and, possibly, the premaxilla (Text-fig. 6A–F).

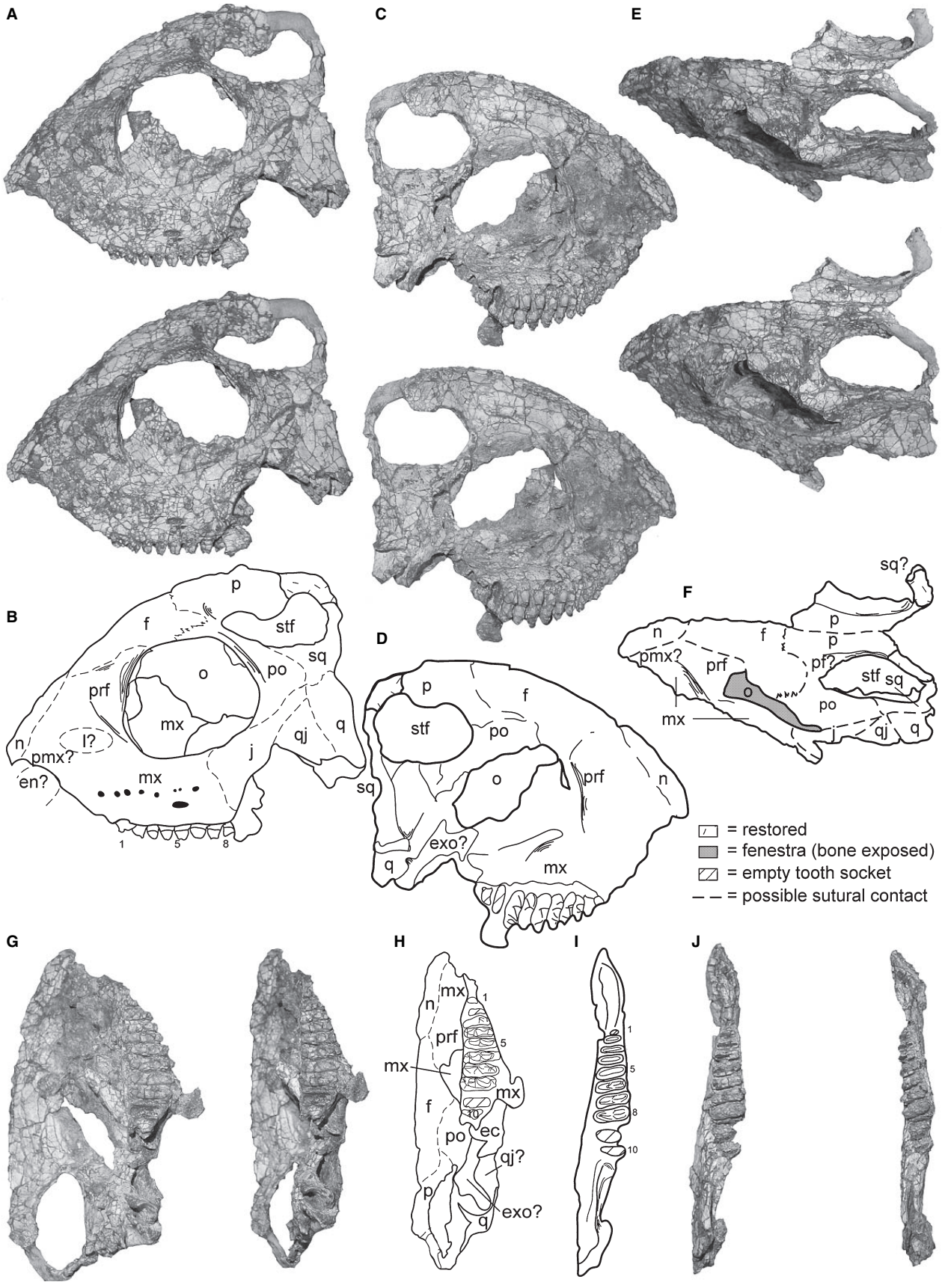
The prefrontal presumably forms most of a laterally projecting rim anterior to the orbit (Text-fig. 6A–F). The bone appears to be roughly triangular in outline, although only its suture with the frontal is distinct.

We infer the presence of a lacrimal based on comparison with the sutural relationships documented by Parks (1969, fig. 3) for *T. buettneri*, but there is no distinct ossification we can identify as such (Text-fig. 6B).

The frontal comprises the largest single bone of the skull roof as preserved. It widens significantly from its anterior sutures with the nasals and the prefrontals and occupies much of the dorsal margin of the orbit. Posteriorly, it has a mediolaterally straight contact with the parietal, but its relationships with the postorbital and the postfrontal are not certain.

The parietals are the best-preserved paired elements of the skull. As noted previously, the parietals form the bulk of the paired parasagittal crests, which are separated by a flat expanse of bone on the skull roof also composed of the parietals. This feature is the most significant non-dental difference between the skulls of *T. jacobsi* and *T. buettneri*. We do not think this is an ontogenetic feature, as it would require substantial restructuring of the parietal itself, including a medial migration of the jaw musculature, to attain the single crest condition seen in *T. buettneri* (compare Text-fig. 6E–F with Gregory 1945, fig. 2). Modesto and Sues (2004) described some variation in the extent to which the jaw adductor musculature attached dorsally on the parietal of the archosauromorph *Prolacerta broomi*. However, the differences we document here are substantially greater between the two species of *Trilophosaurus* recognized here than Modesto and Sues (2004) found in *Prolacerta*, so we feel justified in using the different organization of the adductor crests (sagittal in *T. buettneri*, parasagittal in *T. jacobsi*) as a species-diagnostic feature.

The anterior margin of the dorsal portion of neither squamosal is preserved, but impressions of both are present in the matrix, so we have reconstructed them on both the fossil itself and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prf
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stf
sq
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po
mx
qj
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= restored
= fenestra (bone exposed)
= empty tooth socket
= possible sutural contact
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the illustrations we provide (Text-fig. 6A–H). The squamosals are largely depressed below the level of the skull roof, and form the posterior of much of the ventral margin of the supratemporal fenestra. Anteriorly, the squamosal abuts the postorbital, but the ventral margin of this contact appears to be a complex suture with contacts with the jugal and the quadrate as well.

The contact between the postorbital and the frontal is well defined, but its relationship to the parietal remains ambiguous, although it may form some of the steep wall on the medial rim of the supratemporal fenestra. The postorbital is bordered dorsally by the frontal, where it contacts the orbit, and appears to taper posteriorly along the ventral margin of the supratemporal fenestra.

The jugal is the most clearly delineated bone in the skull, although much of its ventral margin is apparently missing. The anterior margin extends past the posterior end of the tooth margin, but the bone itself overlaps the maxilla and is, of course, not tooth-bearing. It floors only the posteroventral corner of the orbit. Posteriorly, this bone tapers more than that illustrated by Parks (1969, fig. 3) for *T. buettneri*.

Relatively little of the quadratojugal is preserved, but its dorsal contact with the jugal is distinct and indicates that much of the ventral margin of the skull posterior to the tooth row must have been formed by this bone. Thus, it appears likely that the quadratojugal in *T. jacobsi* is a larger ossification (and, conversely, the jugal a smaller one) than its counterpart in *T. buettneri*. This would be even more pronounced if, as restored by Gregory (1945, fig. 4; also pl. 19, fig. 1) for *T. buettneri*, the articulation of the skull with the mandible is depressed below the level of the maxillary tooth row.

Only the dorsalmost projection of the quadrate is preserved, although it is prominently exposed on the lateral surface of the skull as preserved. Its contact with the quadratojugal is straight, rather than curved (as illustrated by Parks 1969, fig. 3).

The mandible was originally found in articulation with the skull, although slightly disarticulated at the mandibular symphysis. The left mandibular ramus is the better preserved (Text-fig. 6I–J), consisting of an essentially complete dentary with 11 tooth positions (nine occupied by teeth) and incomplete surangular, angular and splenial. The right mandibular ramus is broken anterior to the tooth row, such that the symphysial region is missing. The right dentary has 11 unambiguous tooth positions, nine of which are filled by teeth in variable states of preservation, although most are better preserved than their counterparts in the left dentary. The ventral and posterior portions of the mandible are poorly preserved.

The dentary is by far the largest bone in the mandible, and has a complex sigmoid shape from the symphysis, with an anteriorly concave curve between the symphysis and the first tooth and a convex curve wrapping around the tooth row (Text-fig. 6I–J). The first two teeth are small and comparatively simple: the first is a simple peg, and the second has no more than two cusps. Tooth positions 3–9 are occupied by tricuspate, transversely broadened teeth that increase in size posteriorly. Positions 10 and 11 probably bore similar teeth, although the teeth were smaller (less wide) than tooth number 9, based on the size of the broken roots in those positions.

The seven anteriormost tricuspate teeth (positions 3–9) are orientated so that their lingual cusps are anteroposteriorly aligned, and the labial margin of the tooth row is therefore convex, as in the maxilla. The last two tooth positions are deflected somewhat labially. The entire posterior portion of the ramus is therefore orientated at an angle of almost 45 degrees to the tooth row. The surangular is deeply grooved in dorsal (occlusal) view.

The teeth are all *c.* 1·5 mm long. Teeth 3–9 all bear at least the remnants of three cusps, with the labial and the lingual cusps linked to the central cusp by thin, sharp cingula. Where preserved, the central cusp is always the tallest of the three. In occlusal view the central cusp is subtriangular, with the short base lingual to the cusp and the two longer sides mesial and distal, meeting labially to form a point between the central cusp and the labial cusp. The central cusp tends to lie closer to the labial cusp than the lingual cusp. This tooth morphology is identical to that described by Murry (1987) in *T. jacobsi*, even though this specimen is, in linear dimensions, at least an order of magnitude larger than the type of *T. jacobsi* (compare Text-fig. 6 with Text-figs 4–5).

In addition to the juvenile skull and mandible described in the preceding paragraphs, several other specimens we have collected from NMMNH locality 3775 preserve taxonomically significant features. These fossils include several dentulous fragments, including three incomplete mandibles, and four incomplete maxillae.

There are six teeth in one maxillary fragment (NMMNH P-29959) we assign to *Trilophosaurus jacobsi* that was illustrated by Heckert *et al.* (2001, fig. 2a). The teeth are slightly damaged, but all are clearly transversely expanded and bear three cusps, one central and one each at the lingual and labial margins. The cusps are sharply pointed and aligned in a row connected by thin transverse cingula. The teeth are tightly packed and aligned medially, with narrower teeth anteriorly and broader teeth posteriorly, thus forming a labially convex tooth margin. Comparison with both specimens and illustrations of *Trilophosaurus buettneri* (Gregory 1945, figs 3, 6; Parks 1969, fig. 2) suggest that this element probably represents the anterior portion of the tooth battery of a left maxilla. However, it is also possible that it is the anterior portion of the tooth battery of a right dentary. In general, the maxilla of *Trilophosaurus* demonstrates a greater increase in the width of teeth posteriorly than does the dentary, so this element is most likely a left maxilla.

TEXT-FIG. 6. A, C, E, G, J, photographs and B, D, F, H–I, interpretative sketches of a juvenile skull and mandible (NMMNH P-41400) of *Trilophosaurus jacobsi* Murry from NMMNH locality 3775. A–H, incomplete skull in A–B, stereo left lateral, C–D, stereo medial, E–F, stereo dorsal, and G–H, stereo ventral views. I-J, left mandibular ramus in stereo dorsal (occlusal) view. All × 0·8. Numbers refer to tooth positions. Abbreviations: ect, ectopterygoid; en, external naris; exo, exoccipital; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; o, orbit; p, parietal; pf, postfrontal; pmx, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal; stf, supratemporal fenestra.

One of the more striking features of NMMNH P-29959 is the close spacing of the teeth. Published illustrations and comparable specimens of *Trilophosaurus buettneri* from the WPA localities indicate that the teeth are much closer together in NMMNH P-29959 than in the TMM specimens. Similarly, the teeth of NMMNH P-29959 are also much closer together than in the holotype of *T. buettneri* (Text-fig. 3). This may represent an additional diagnostic feature of *T. jacobsi*.

Another tooth illustrated by Heckert *et al.* (2001, fig. 3a), NMMNH P-29960, is similarly broad transversely, although the labial and the medial cusps are broken. Cingula are present on both the mesial and distal margins of this tooth, and evident on the teeth of NMMNH P-29959 as well. Clearly, this tooth is morphologically similar to those of NMMNH P-29959. The tooth crown is relatively tall, and there is a substantial root that is nearly as tall as the crown. Where the central cusp is preserved, including NMMNH P-29960, it is particularly swollen mesiodistally, so that the lower slopes of the central cusp divide the mesial and distal cingula into labial and lingual segments. This swollen base of the central cusp differs from that of both the type and the WPA specimens of *T. buettneri* and appears to be unique to *T. jacobsi*. Damage to the teeth of NMMNH P-29959 and P-29960 prevents us from describing detailed features, such as possible wear facets, with confidence. It is important to note that both P-29959 and P-29960 are substantially larger than P-41400, yet still have a similar overall tooth morphology, especially in terms of the presence and distribution of cingula. This indicates that the tooth characters used to differentiate *T. jacobsi* from *T. buettneri*, both by Murry (1987) and as used here, are valid taxonomic differences and not a result of ontogenetic variation (contra Elder 1978, 1987 and DeMar and Bolt 1981).

Remarks. Murry (1987, p. 774) diagnosed *T. jacobsi* from *T. buettneri* based on the following characters: '… relatively smaller size, development of prominent medial and lateral cingula on each cusp, the asymmetrical placement of the central cusp, the successive development of a large central cusp on the posterior teeth, and the possible presence of a large, bulbous tooth on the posterior-most portion of the tooth row with numerous accessory cusps and prominent cingula. Also, the morphology of the jaws suggests that there was no edentulous beak as seen in the premaxilla and dentary of the large Otis Chalk *Trilophosaurus* skulls …'

In *Trilophosaurus jacobsi*, both the dentary and the maxilla are extremely thin immediately anterior to the tooth row, posterior to the bulbous symphysis and anterior to the tooth row. We hypothesize that the holotype of *T. jacobsi* is thus broken at the most anterior point, and therefore only appears to be more dentulous than the anterior parts of upper or lower jaws of *T. buettneri*. Murry (1987) and Sues and Olsen (1993) noted that the tooth row is canted in different directions in the holotypes of *T. buettneri* and *T. jacobsi*. We suspect that the fragmentary holotype of *T. jacobsi* is thus actually a left maxilla, not a right dentary. If this is the case, then much of Murry's (1987) diagnosis of *T. jacobsi* is rendered inaccurate. We note here, however, that the differences in tooth crown morphology are sufficient to diagnose *T. jacobsi* from *T. buettneri*.

The juvenile specimen we document here is much larger than any of the type series of *T. jacobsi*, and well within the size range of *T. buettneri*, including the 'small specimens' from the Otis Chalk quarries. Indeed, this specimen is similar in size to the type of *T. buettneri*. We have not yet ascertained the maximum size of *T. jacobsi*, but the maxilla illustrated by Heckert *et al.* (2001) and redescribed above (NMMNH P-29959) bears teeth similar in size to the largest specimens of *T. buettneri*. The differences in tooth morphology noted by Murry (1987) are indeed valid, and we have expanded on these here. Note also that there is no evidence of ontogenetic change in tooth morphology in *Trilophosaurus*, as demonstrated by the preserved ontogenetic series of *T. buettneri* from the Otis Chalk quarries (Gregory 1945; Parks 1969; DeMar and Bolt 1981) and *T. jacobsi* from NMMNH locality 3775 documented here.

Kaye and Padian (1994, fig. 9.59) illustrated an edentulous jaw fragment they identified as *Trilophosaurus* sp. We have re-examined the specimen and agree that it pertains to *Trilophosaurus*, but is not diagnostic to species. If it pertains to *T. jacobsi*, it is a topotype specimen of that taxon.

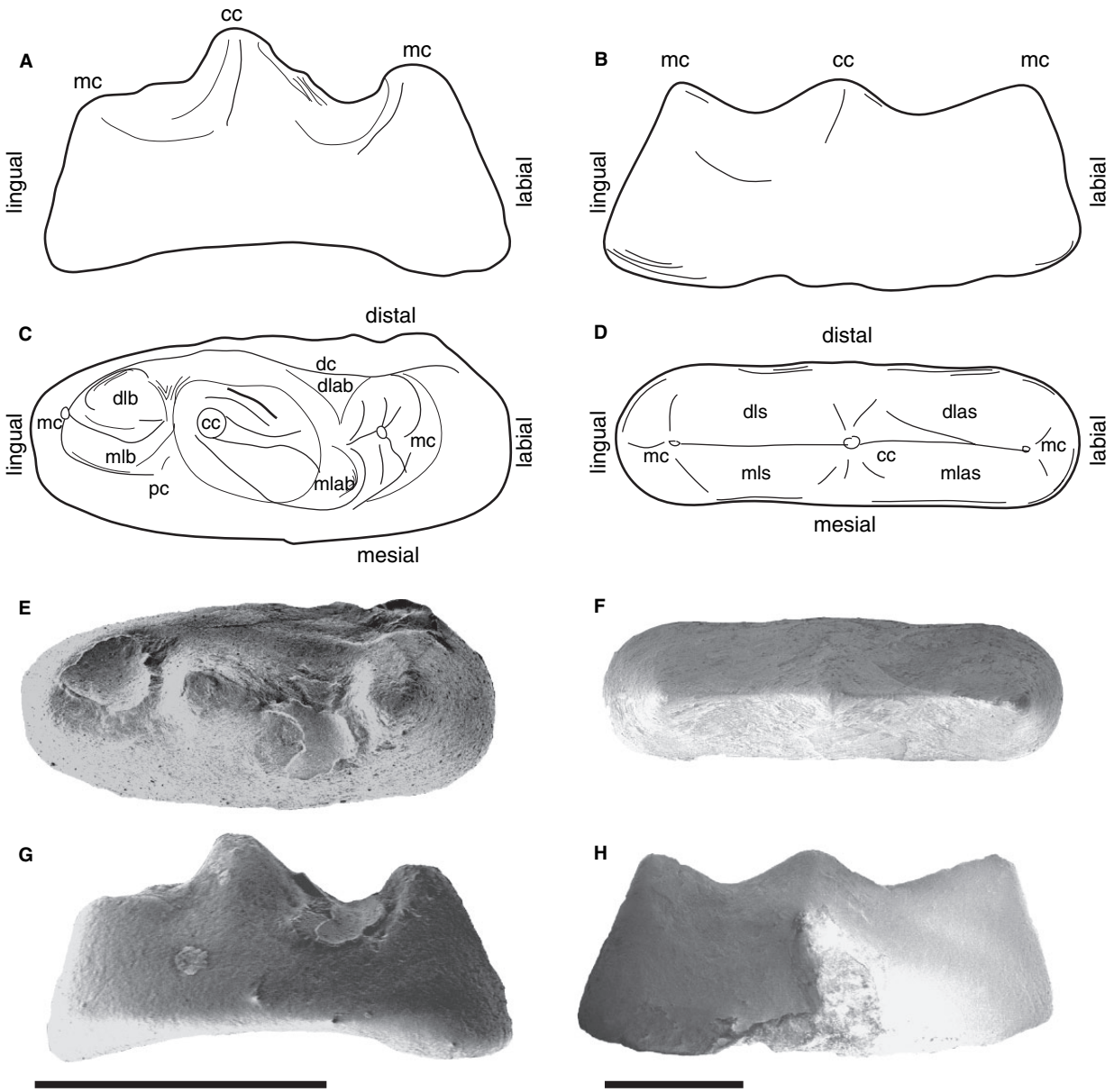
SYSTEMATICS AND TOOTH NOMENCLATURE

The principal systematic aim of this paper is to demonstrate that *T. jacobsi* is indeed closely related to *T. buettneri*. Sues (2003) and Modesto and Sues (2004) were the most recent to include the latter in a comprehensive phylogenetic analysis and, like Dilkes (1998) and most other workers, found that *Trilophosaurus* is an archosauromorph outside of crown-group Archosauria. Aside from the minor differences in cranial anatomy (paired sagittal crests, proportionately larger orbits) and the numerous complexities in the dentition (explored in greater detail below), *T. jacobsi* is clearly more similar to *T. buettneri* than any other taxon, including *Teraterpeton hrynewichorum* Sues. The skull of *T. jacobsi* illustrated in Plate 3 supports the assertions of Gregory (1945), Parks (1969) and Sues (2003) that *Trilophosaurus* lacks an infratemporal fenestra (contra Merck 1995).

One of the key aspects of our study is the fact that, as suggested by Murry (1982, 1987), the teeth of *Trilophosaurus* are identifiable to species, which has implications for the systematics of these taxa as well as for the biostratigraphical and biochronological utility of both taxa. To facilitate comparison, we propose a standardized

nomenclature of *Trilophosaurus* teeth (Text-fig. 7). *Trilophosaurus* teeth are transversely broadened, with a central cusp flanked by two marginal cusps, the labial and lingual cusps (Text-fig. 7). In *T. buettneri*, the three cusps are connected by a thin ridge or cingulum, the only such ridge on the tooth (Text-fig. 7D, F). Consequently, the areas between the cusps on the mesial (rostral) and distal (or caudal) faces of the tooth are comprised of poorly defined sulci. We term these the mesial labial, mesial lingual, distal labial and distal lingual sulci, respectively. The central cusp, marginal cusp, connecting cingulum and these sulci thus comprise the identifiable features of *T. buettneri* tooth crowns.

The teeth of *T. jacobsi* are considerably more complex, and the nomenclature we propose here is designed to elucidate and describe that complexity (Text-fig. 7). As in *T. buettneri*, there is a central cusp, although it is typically displaced somewhat labially and is also generally taller



TEXT-FIG. 7. Isolated teeth of *Trilophosaurus* documenting the differences that distinguish *T. jacobsi* (NMMNH P-34073; A, C, E, G) from *T. buettneri* (NMMNH P-34291; B, D, F, H). Teeth are in rostro-caudal (A–B, G–H) and occlusal (C–F) views. Abbreviations: cc, central cusp; dc, distal cingulum; dlab, distal-labial basin; dlas, distal-labial sulcus; dlb, distal-lingual basin; dls, distal-lingual sulcus; mc, marginal cusp; pc, mesial cingulum; plab, posterolabial basin; plas, posterolabial sulcus; plb, posterolingual basin; pls, posterolingual sulcus. Scale bars represent 1 mm.

than the marginal cusps, which we still identify as the labial and lingual cusps. The three cusps are still connected by a transverse cingulum. However, there are also cingula across the mesial and distal faces of the tooth, and we term these the mesial and distal cingula. As a result, there are well-defined basins in the same (homologous) area where there are only sulci on *T. buettneri* teeth. Consequently, on *T. jacobsi* teeth we identify mesial labial, mesial lingual, distal labial and distal lingual basins, each lying between the transverse cingulum and the marginal (mesial or distal) cingulum. Two other cingula lie on the labial face of the central cusp, one extending down to the mesial cingulum and the other to the distal cingulum. These cingula, combined with the asymmetrical shape and offset of the central cusp, render even fragmentary fossils diagnostic of *T. jacobsi*. Indeed, these cingula are evident in the one well-preserved tooth on the holotype of *T. jacobsi*, so regardless of its identification as a right dentary (Murry 1987) or left maxilla (this paper), the distinction between the two species of *Trilophosaurus* is readily discerned on the two type specimens.

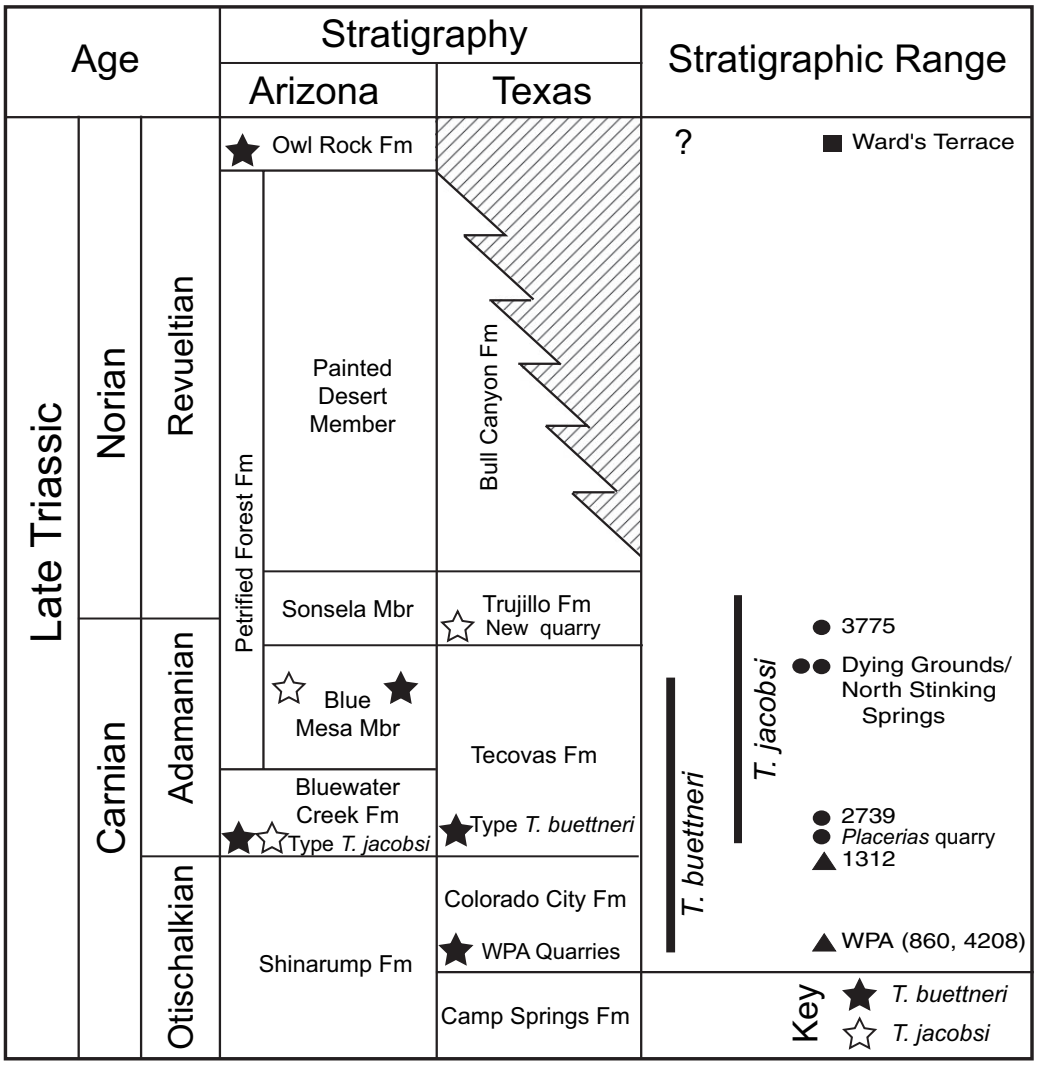
BIOSTRATIGRAPHY AND BIOCHRONOLOGY OF *TRILOPHOSAURUS*

The numerous differences in tooth morphology between *T. buettneri* and *T. jacobsi* show that either taxon can be identified from a fragment of one of the primary teeth. One implication of this is that, for the first time in the Upper Triassic of the American South-West, it is possible to erect and utilize a tooth-based biostratigraphy similar to typical mammal-based biostratigraphical schemes for Upper Cretaceous and Cenozoic strata. In addition, the geographical and stratigraphical range of both *Trilophosaurus* species can now be evaluated.

Trilophosaurus buettneri is, with the possible exception of a single specimen, restricted to the lowermost part of the Chinle Group. Detailed stratigraphical data are lacking for the type specimen, but strata exposed in the area where the type was collected pertain to the lower Tecovas Formation (Long and Murry 1995). The fauna associated with the type specimen includes the lungfish *Arganodus* sp., the metoposaurid *Buettneria perfecta* Case, the aberrant amniote *Colognathus obscurus* (Case), and the aetosaurs *Stagonolepis wellesi* (Long and Ballew) and *Desmatosuchus haplocerus* (Cope) (Murry 1986; Long and Murry 1995). *Stagonolepis* is an index taxon of the Adamanian LVF of Lucas and Hunt (1993; Lucas 1998), so this assemblage is of Adamanian age (Text-fig. 8).

All workers (except Lehman 1994) agree that the WPA quarries, which yield solely *T. buettneri*, are stratigraphically very low in the Chinle Group (Elder 1978, 1987; Murry 1982, 1986; Chatterjee 1986; Lucas *et al.* 1994; Long and Murry 1995). Indeed, the tetrapod fauna associated with the WPA quarries and surrounding area is the type fauna of the Otischalkian LVF of Lucas and Hunt (1993; Lucas 1998), and includes records of the metoposaurid *Metoposaurus*, the phytosaurs *Angistorhinus* and *Paleorhinus*, and the aetosaur *Longosuchus*, among other tetrapods. This fauna is, by definition, Otischalkian in age, and includes the Otischalkian index taxa *Metoposaurus*, *Paleorhinus* and *Longosuchus*. The only other specimens of *T. buettneri* are isolated teeth from the Kalgary microvertebrate localities and the Petrified Forest National Park. Murry (1982, 1986) identified several teeth of *T. buettneri* from the lower Kalgary microvertebrate locality. Heckert (2001, 2004) also reported *T. buettneri* from that locality as well as from the upper Kalgary microvertebrate locality. The Kalgary sites are near the base of the Tecovas Formation. The lower Kalgary site may be as old as Otischalkian (Heckert 2001, 2004) but the upper Kalgary locality is clearly of Adamanian age, as the associated fauna includes the phytosaur *Rutiodon* and the aetosaur *Stagonolepis*, both index taxa of the Adamanian LVF (Lucas and Luo 1993; Long and Murry 1995). Murry (1989, fig. 7h) illustrated a single tooth of *T. buettneri* from the 'Dying Grounds' locality at the Petrified Forest National Park. The Dying Grounds is in the Blue Mesa Member of the Petrified Forest Formation, and the Dying Grounds fauna is part of the type fauna of the Adamanian LVF of Lucas and Hunt (1993; Lucas 1998). This is the stratigraphically highest confirmed record of *T. buettneri*.

The only other fossils referred to *T. buettneri* are those identified by Kirby (1989, 1991, 1993) from the Owl Rock Formation near Ward's Terrace in north-central Arizona. These records were based on an isolated tooth and several fragmentary skull bones. We concur that the incomplete tooth, MNA V7064, could represent *Trilophosaurus*, but it also closely resembles *Tricuspisaurus*, a possible procolophonid known from fissure fills of similar age in Britain (Robinson 1957; Fraser 1986). Indeed, a derived leptopleurine procolophonid is known from the same unit (Sues *et al.* 2000). MNA V7064 is broken and only preserves two cusps. There are no distal or mesial cingula, and the preserved cusps are subequal in size and shape. These characteristics preclude assignment to *T. jacobsi* and support assignment to *T. buettneri*. We are hesitant to do this, however, as it would be an incredible range extension for the taxon. We note two alternative interpretations: (1) MNA V7064 actually pertains to another taxon with multicuspid teeth, perhaps a procolophonid; or (2) it is a tooth of *T. buettneri*, but represents contamination from another screenwashing site. In support of the first hypothesis, MNA V7064 and *Tricuspisaurus* are less transversely broad than referred specimens of *Trilophosaurus*,



TEXT-FIG. 8. Generalized stratigraphic distribution of *Trilophosaurus* occurrences in the south-western USA. See text for discussion. Localities as in Text-fig. 1.

and thus more closely resemble teeth of procolophonids. The sole evidence supporting the second hypothesis is the fact that Kirby performed his work at the MNA in the mid- to late 1980s, and Tannenbaum (1983) had earlier completed a master's thesis based on MNA's microvertebrate collections obtained by screenwashing the *Placerias* quarry. Therefore, we consider the apparent Owl Rock record of *Trilophosaurus buettneri* to be unreliable.

T. jacobsi teeth are even more distinct and recognizable as minute fragments. The type locality, the *Placerias* quarry in eastern Arizona, is low in the Bluewater Creek Formation (Lucas *et al.* 1997) and yields many isolated teeth in addition to the tooth-bearing jaw fragments in the type series identified by Murry (1987). Murry (1982, 1986) was aware of the difference between teeth of *T. buettneri* and *T. jacobsi*, and in 1982, referred to teeth of *T. jacobsi* as '*Variodentoides jacobsi*', although later he (Murry 1987) referred only specimens from the type locality to *T. jacobsi*. Sues and Olsen (1993) did not refer any additional specimens to *T.* (= *Chinleogomphius*) *jacobsi*, nor did Long and Murry (1995). Heckert (2001, 2004) identified isolated teeth of *T.* (= *Chinleogomphius*) *jacobsi* from both the upper Kalgary microvertebrate localities as well as from the lower Bluewater Creek Formation in western New Mexico, and we illustrate some of these specimens here (Text-fig. 7). We also assign some of the specimens Heckert (2001) identified as 'Procolophonidae indet.' to *T. jacobsi*. A preliminary report on the fauna of NMMNH locality 3775 by Heckert *et al.* (2001) generally did not identify the specimens to species, but did note the variations in size and considered the fossils from locality 3775 to represent the larger morph. With more material at hand it is now clear that (1) the specimens from locality 3775 pertain to *T. jacobsi*; and (2) they represent a growth series of *T. jacobsi*.

Detailed investigation of specimens assigned to *Trilophosaurus* thus demonstrates that *T. buettneri* is restricted to strata of Otischalkian–early Adamanian age, and that *T. jacobsi* occurs in strata of Adamanian and, possibly, earliest Revueltian age. It is therefore apparent that both taxa have biostratigraphical utility, because the teeth are identifiable as isolated fossils.

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